Capuchin monkeys are sensitive to others' welfare

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Humans demonstrate altruistic behaviors in a variety of contexts [1,2], but there is growing experimental evidence that our closest living primate relative, the chimpanzee, does not always share our human prosocial tendencies [3,4]. Although chimpanzees behave cooperatively in some contexts, there is growing evidence that chimpanzees are indifferent to others' needs when food is involved. Indeed, a number of studies have shown that chimpanzees fail to selectively donate food to others even when they do so at no cost to themselves [3,4]. Chimpanzees' lack of other-regarding preferences in these recent studies had initially caused many researchers to conclude that humans are alone in our capacity for prosocial giving. Researchers have therefore begun exploring *why* humans' prosociality differs from that of closely-related primates, leading some to observe that humans' prosocial tendencies might stem specifically from their history as reproductively cooperative breeders (see [5,6] for evidence of prosocial giving in cooperatively breeding primates). Here, we test this claim directly, providing a surprising demonstration that one non-cooperative breeder, the tufted capuchin monkey (*Cebus apella*), reliably exhibits prosocial behavior in a food-sharing task modeled after a human economic task known as the Dictator Game [2].

Capuchins (n = 7) could pull one of two wooden planks that could deliver food to two side-by-side chambers (Figure 1). Food placed on the left side of the planks could be accessed only in the chamber where the subject was positioned (the proposer's chamber), while food placed on the right side could be accessed only from the second chamber (the receiver's chamber). Only the subject monkey in the proposer's chamber could pull and operate the planks. We kept the proposer's payoffs constant across the two planks but varied the size of the payoffs to the receiver's chamber to investigate if and when capuchins were willing to provide the receiver's chamber with a large reward (a marshmallow) instead of a small reward (a celery piece). This led to two kinds of trials: ones in which the proposer delivered marshmallow to his own chamber and chose either marshmallow or celery for the receiver's chamber, and ones in which the proposer delivered celery to his own chamber and chose either marshmallow or celery for the receiver's chamber. We then compared monkeys' likelihood of delivering the larger reward in a condition in which a receiver monkey was present (*test condition*) to one in which no monkey was present (*empty control condition*) and another in which no monkey was present and an opening allowed the subject to access rewards in the receiver's chamber (*selfish control condition*).

In contrast to work in chimpanzees [3,4] and the predictions of a cooperative-breeding account [5], we observe reliable prosocial behavior in capuchins. Subjects were more likely than chance to deliver the better marshmallow reward to the receiver's chamber when a receiver was present, as shown through a two-tailed one sample t-test ($t(6) = 3.47$, $p < 0.01$) (Figure 2). Monkeys also delivered larger rewards on the selfish control ($t(6) = 5.55$, $p < 0.001$), but not on the empty control condition ($t(6) = 1.73$, $p = 0.13$). Further examining this pattern, we confirmed using one-tailed t-tests that monkeys donated the larger marshmallow reward reliably more

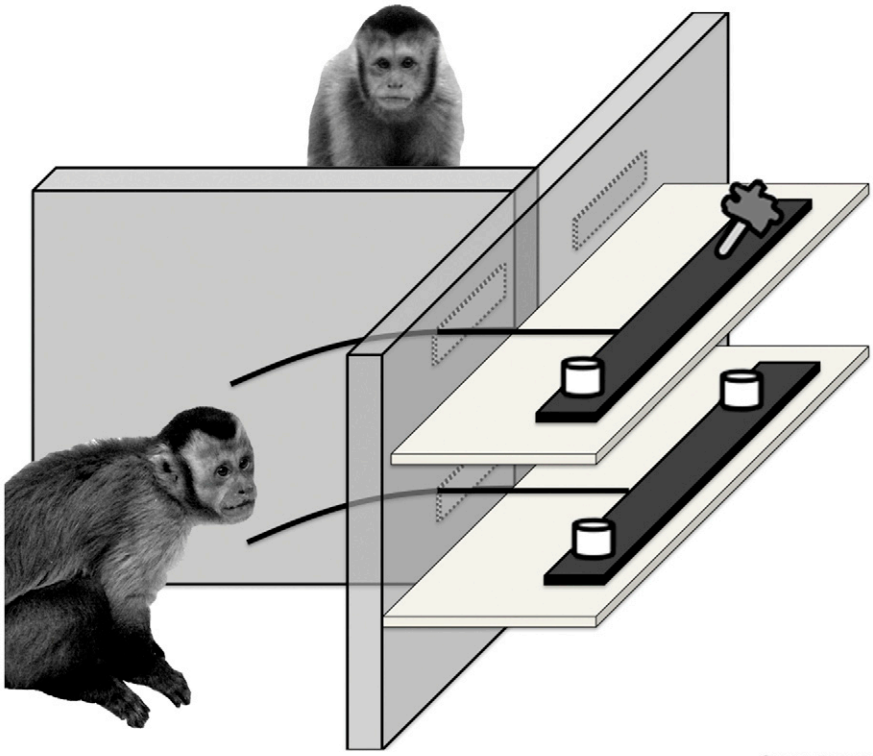

Figure 1. The experimental set-up in the test condition.

The apparatus consisted of two wooden shelves each containing a plank baited with food. Only the monkey playing the role of the proposer (in this case, the monkey on the left) had access to ropes which could move either plank toward the enclosures. In this way, the proposer (but not the receiver) could select which plank would deliver food. The two planks always provided the same reward to the proposer's side (in this case, marshmallow), but differed in the rewards provided to the receiver (here, the top plank delivers celery, and the bottom plank delivers marshmallow). This set-up could be modified so that the recipient monkey was not present (the *empty control condition*), and additionally modified so that the proposer monkey could reach into the receiver's chamber, thus allowing the proposer monkey to collect any food rewards delivered to this chamber (the *selfish control condition*).

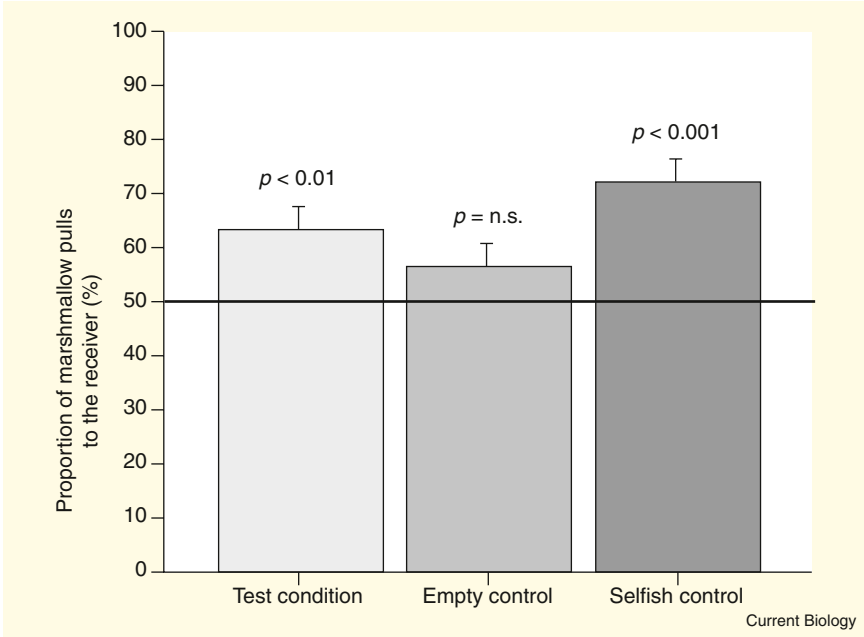

Figure 2. Proportion of large reward (marshmallow) deliveries across all three conditions.

The proportion of trials in which proposers chose to provide a receiver with marshmallow rather than celery is plotted on the y-axis, and condition type is plotted on the x-axis. Subjects delivered the marshmallow more than chance on the selfish control condition ($t(6) = 5.55$, $p < 0.001$) and the test condition ($t(6) = 3.47$, $p < 0.01$), but not on the empty control condition ($t(6) = 1.73$, $p = 0.13$).

often when a receiver monkey was present than when he was absent (Mean Difference: 8.1%, $t(6) = 1.91$, $p = 0.05$). Monkeys donated the larger reward slightly but not significantly less often when a receiver monkey was present than in the selfish control condition in which the proposer monkey could receive the larger reward himself (Mean Difference: 12.6%, $t(6) = 1.77$, $p = 0.06$).

The monkeys' performance on the control conditions demonstrated that they understood the nature of the pulling task, showing significantly more deliveries of the larger reward in the selfish control condition than in the empty control condition (Mean Difference: 20.6% marshmallow pulls, $t(6) = 4.99$, $p = 0.001$). Importantly, however, the proposer's personal payoff — receiving marshmallow *versus* celery — had no effect on subjects' prosocial tendencies ($F(2,12) = 1.56$, $p = 0.25$). That is, monkeys significantly donated the marshmallow reward to their partner *even* in conditions in which they themselves received the celery reward. This result suggests that capuchins continue to demonstrate prosocial tendencies even in cases in which the receiver's payoff is larger than the one the proposer is allowed to keep for himself. This is especially striking given capuchins' known tendency to evaluate their rewards in relative terms [7–9], and to reject rewards that are relatively smaller than those of another monkey [7]. Indeed, humans exhibit diminished regard for others in situations in which actors receive rewards that are relatively smaller than those given to receivers (for example [10]), contrasting with the rates of giving we observed in capuchins.

Our results show that capuchins reliably give food to other individuals in a limited-form Dictator Game, providing the first evidence that a non-cooperatively-breeding species shares human prosocial tendencies. In fact, capuchins' prosociality persists even in the most stringent case in which a proposer's prosocial choice results in the receipt of a relatively smaller personal reward. These results raise the possibility that prosociality may be broadly shared throughout the primate order despite its conspicuous absence in chimpanzees [3,4], and thus demonstrate that ecological factors other than cooperative breeding underlie the emergence of altruism in humans.

Supplemental Data

Supplemental data are available at http://www.current-biology.com/supplemental/S0960-9822(08)01135-4.

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